

Blood Oxygen Conservation in Diving Sea Lions: How Low Does Oxygen Really Go?

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LONG-TERM GOALS

California sea lions (*Zalophus californianus*) from San Nicolas Island regularly perform 350-meter deep dives during maternal foraging trips to sea. The physiology of these extreme dives is relevant to the development of the sea lion as a model to investigate deep diving physiology and the avoidance of decompression sickness in a marine mammal. Such a model is essential to better understand the potential role of decompression sickness in the etiology of the stranding of beaked whales after exposure to naval sonar as well as to evaluate the value and accuracy of the many numerical models of nitrogen uptake and distribution in these animals. This project continues prior physiological investigations with these animals and focuses on the relationship of blood oxygen depletion patterns during dives to heart rate and muscle workload.

OBJECTIVES

With techniques and backpack data recorders developed in prior ONR-funded research, this project will a) compare blood oxygen depletion profiles in the anterior and posterior venae cavae of diving sea lions, and b) investigate the effects of heart rate and flipper stroke rate on simultaneously recorded venous oxygen depletion patterns during dives. The goals of this research are to a) document the magnitude and pattern of depletion of the entire venous oxygen store during dives, b) examine the effect of muscle work load (flipper stroke rate) and potential blood oxygen extraction by muscle on the simultaneously recorded venous oxygen depletion profiles in both the anterior and posterior venae cavae, and c) determine the effect of heart rate and potential perfusion-related blood oxygen extraction by tissues on the simultaneously recorded venous oxygen depletion profiles in both the anterior and posterior venae cavae.

APPROACH

Objective 1: In order to calculate the rate and magnitude of depletion of the blood O₂ store during dives, P_{O₂} profiles will be obtained from a P_{O₂} recorder and intravascular electrode deployed on sea lions (McDonald and Ponganis 2012). The P_{O₂} electrode will be placed in either the anterior or posterior vena cava. As in previous research by the PI with California sea lions and other species

(McDonald and Ponganis 2013; Meir et al. 2009; Meir and Ponganis 2009), the P_{O_2} profiles will be converted to Hb saturation profiles with the use of the sea lion O_2 -Hb dissociation curve. In addition to the P_{O_2} and Hb saturation profile during a dive, the start-of-dive and end-of-dive % Hb saturations can then be used to calculate the magnitude of blood O_2 depletion during dives based on the net change in % Hb saturation, and the known Hb concentration and blood volume.

Objective 2: ECG profiles will be simultaneously collected from freely diving sea lions equipped with a P_{O_2} electrode in either the anterior or posterior vena cava in order to assess the rate of venous O_2 desaturation to heart rate throughout dives.

Objective 3: Accelerometers will be deployed on freely diving sea lions equipped with a P_{O_2} electrode in either the anterior or posterior vena cava in order to assess the rate of venous O_2 desaturation to work load (stroke rate or MSA) throughout dives.

WORK COMPLETED

The second field season of this grant has just been completed. Analysis of these data and prior studies from the previous field season are underway. Initial results were presented at the 2014 Bio-logging Conference; two oral presentations will also be made at the 2015 Marine Mammal Conference.

RESULTS

As in a pilot study from the prior ONR grant, the P_{O_2} and Hb desaturation profiles in the anterior and posterior venae cavae are different (Fig. 1), but end-of-dive saturations approximate the same 20-30% region of saturation.

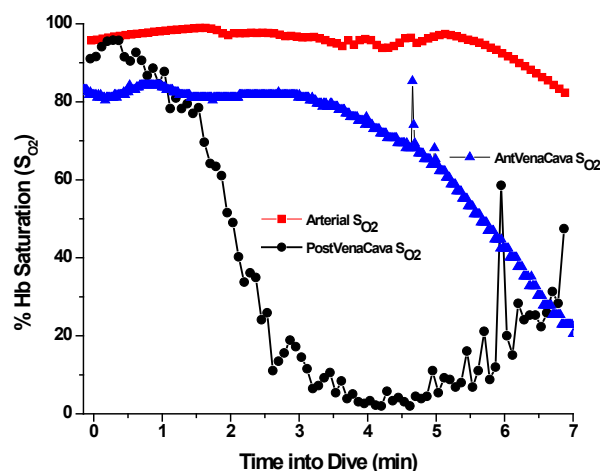


Figure 1. Arterial, anterior vena caval, and posterior vena caval hemoglobin (Hb) saturation profiles during 380-m deep dives of California sea lion. Each profile is from a different sea lion.

Analyses of venous hemoglobin saturation profiles and simultaneously paired heart rate or stroke rate profiles are in progress. A stroke rate analysis program has been developed and is undergoing further refinement. Review of posterior vena caval desaturation rates relative to stroke rate in all dives (Fig. 2) reveals a highly variable relationship, suggesting that posterior vena caval desaturation is not related to muscle workload.

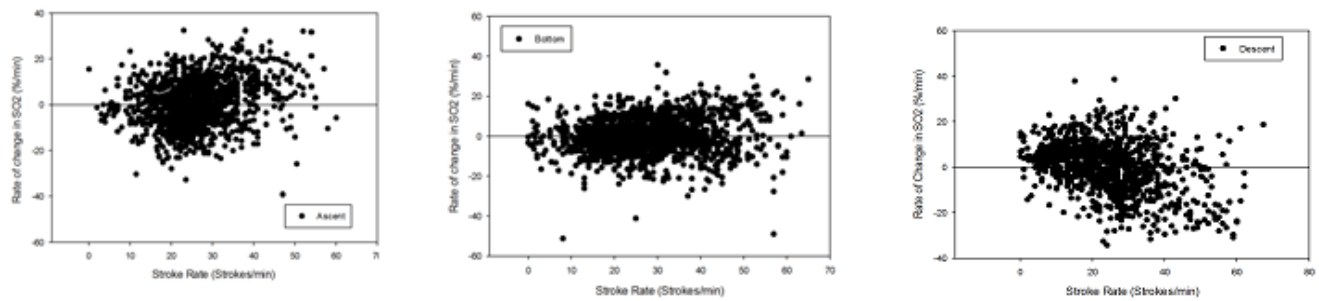


Figure 2. Rate of change in posterior venacaval hemoglobin saturation (S_{O_2}) in relation to stroke rate during descent, bottom phase, and ascent of all dives of sea lions.

Initial analysis of caudal gluetail vein P_{O_2} profiles obtained with a shorter P_{O_2} electrode than those in prior studies has revealed striking arterialization of venous blood in deep dives, indicating that the shorter electrode is probably in a vein draining from an arterio-venous shunt. This is an extremely valuable documentation of a-v shunting in diving sea lions as such shunts will not only influence oxygen store depletion patterns but will also effect nitrogen distribution and absorption kinetics. The utilization of arterio-venous shunts during dives has implications for the risk of decompression sickness and for the accuracy of the many numerical models of nitrogen uptake and distribution. None of the models incorporate potential effects of arterio-venous shunting.

IMPACT/APPLICATIONS

In prior ONR-funded research, partial pressure of oxygen (P_{O_2}) profiles provided evidence that lung collapse occurred near 200-m depth in diving sea lions (McDonald and Ponganis 2012). This impairment of gas exchange limits nitrogen uptake at depth and preserves lung oxygen for later use during ascent. More recent research has revealed that heart rate rapidly declines during descent of deep dives to values less than 10 beats min^{-1} (McDonald and Ponganis 2014). Such a low heart rate also limits the absorption and distribution of both nitrogen and oxygen at depth (through reductions in pulmonary and aortic blood flow). As a result of these physiological processes, the sea lion can maintain arterial hemoglobin saturation above 90% during deep dives as long as 7 minutes (McDonald and Ponganis 2012; McDonald and Ponganis 2013). In contrast, the elephant seal (*Mirounga angustirostris*), which dives on expiration and has less than 5% of total body O_2 stores in the respiratory system, experiences significant hypoxemia with routine arterial hemoglobin desaturation to 10 to 20% (Meir et al. 2009). However, similar to the sea lion, the emperor penguin (*Aptenodytes forsteri*), another animal that dives on inspiration with a large respiratory O_2 store, also can maintain arterial saturations during dives as long as 10 min (Meir and Ponganis 2009). It is also notable that a severe bradycardia during descent occurs in deep-diving emperor penguins (Ponganis, unpublished data), and in deep-diving bottlenose dolphins (*Tursiops truncatus*), which also dive on inspiration (Houser et al. 2010; Williams et al. 1999). For these reasons, it is hypothesized that the heart rate profile during deep dives of California sea lions is universal among higher vertebrates that dive on inspiration. Hence, both lung collapse and the heart rate profile make the California sea lion a valuable model to investigate physiological responses and gas uptake / distribution during deep dives.

The lower heart rates during deeper, longer dives observed in this study and the lack of complete blood oxygen depletion during these deep dives that were documented in our prior ONR study (McDonald and Ponganis 2012; McDonald and Ponganis 2013) also have implications for the management of oxygen stores and the physiological basis of the ADL. The concept that most dives are aerobic in nature and do not exceed an aerobic dive limit (ADL - dive duration associated with the onset of post-dive blood lactate accumulation) has dominated the interpretation of dive behavior and foraging ecology over the past 30 years (Costa et al. 2001; Kooyman et al. 1980). However, because of technical difficulties, the ADL has rarely been measured. Instead, researchers have had to resort to estimations of total O₂ store depletion, i.e., calculated ADLs (cADLs) (Costa et al. 2001; Weise and Costa 2007). Our findings in sea lions have supported the concept that the physiological basis of the ADL is muscle oxygen depletion and subsequent glycolysis. The lung and blood oxygen stores are not completely depleted in even the longest of sea lion dives. The severe bradycardia during deep dives contributes to the preservation of the blood and lung oxygen for use during ascent, and it also creates greater reliance of muscle metabolism on the myoglobin-bound muscle oxygen store. In addition, the lack of correlation between heart rate and stroke rate during deeper dives (Figs. 1 and 3) suggests that muscle blood flow and oxygen delivery are not coupled with stroke effort. These findings reinforce our hypothesis that depletion of the muscle oxygen store with subsequent glycolysis underlies the ADL.

This current project will address the linkage of venous blood O₂ depletion to heart rate and to muscle work load (stroke rate and other indices of stroke effort). Furthermore, it will examine blood O₂ depletion in both the anterior and posterior vena cavae. These analyses will allow documentation of the degree of depletion of the entire venous O₂ store, and reveal which factor (heart rate or stroke rate) that depletion is most dependent upon. Such analysis will further document the potential relation of heart rate and muscle blood flow to muscle workload during dives, and to the physiological model of the ADL discussed in the prior paragraph.

RELATED PROJECTS

This project is building on our findings from our previous ONR funded projects: “Blood oxygen depletion in California sea lions: How close to the limit?” (award #: N000141010514), and “Deep diving California sea lions: Are they pushing their physiological limits?” (award #: N000141210633).

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